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Changes in the collembolan community during the decomposition of needle litter in a coniferous forest

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Summary. Changes in the collembolan community were studied during the decomposition of conifer needles. Organic matter, nitrogen and carbon mass, and collembolan populations in litter bags, were monitored over a 5 year period. Decomposition of *Chamaecyparis obtusa* needle litter was represented by three phases; the initial leaching of nitrogen (0–3 months), nitrogen immobilization (3–200 months), and nitrogen mobilization (20–60 months) and thus provided three resource states for the colonization of collembolan species. The species composition of the collembolan community in the soil was constant over the study period, while the litter bag communities showed seasonal and successional changes. According to the successional patterns, collembolan species were classified into three groups; the species occurring in the immobilization phase, the species abundant during the immobilization and mobilization phases, and the species occurred in the mobilization phase. The successional changes of Collembola may be explained through immigration and emigration of species into or from the litter bags in response to the litter fall supply and decomposition phases. The litter bag study suggests that the collembolan community might be maintained at an equilibrium state through the responses of individual species to the litter fall supply and decomposition process.

Key words: Carbon and nitrogen dynamics, Collembolan community, decomposition, immobilization, litter fall, mobilization

Introduction

Community organization of soil animals has been explained in terms of the feeding and habitat preferences of species in soils (e.g. Anderson 1975; Petersen & Luxton 1982; Takeda 1987). In forest ecosystems, plant litter provides material for food and microhabitats for soil animals and is modified thorough the decomposition in soils (Takeda, 1995 a). So, soil animal populations are organized into the communities in response to resource dynamics represented by litter supply and decomposition processes. Changes in litter bag fauna during the decomposition of litter have been studied to explain the organization of soil animal communities in soils. Succession patterns have been shown in number of soil arthropods including Cryptostigmata, other Acari and Collembola (Anderson 1975; Huhta et al. 1979; Hågvar & Kjøndall 1981; Takeda, 1987, 1988). The successional changes of soil animals have been explained by the individual responses of species to the food and habitat conditions of decomposing litter (Anderson 1975; Takeda 1987). The objectives of this study are to show the changes in collembolan communities during the decomposition of needle litter characterized by the leaching, immobilization, and mobilization phases of nitrogen (Berg & Staaf 1981; Takeda 1995b). The successional changes of collembolan

communities were explained in terms of the responses of collembolan species to litter fall and to the three decomposition phases. The roles of collembolan species are discussed in relation to the decomposition phases of *Chamaecyparis obtusa*. Endl. needles.

Materials and Methods

Site description

The study was carried out in a natural forest of *Chamaecyparis obtusa* at Kamigamo Forest Experimental Station of Kyoto University, about 12 km north of Kyoto City (35.4′ N and 135.43′ E). The canopy trees mainly consist of *Chamaecyparis obtusa*. Endl. and the understory of deciduous trees and *Chamaecyparis obtusa* saplings. The forest is situated on a gentle hill slope at 200 m altitude. A study plot of 10×20 m was laid out in the forest and was used for the sampling of soil animals and for the litter bag study.

Meteorological data were obtained from the Station. Mean annual precipitation and evaporation were 1678 mm and 986 mm respectively. Mean monthly temperature ranged from 2.3 °C in February to 28.5 °C in August with a mean of 15 °C over the study period. The litter layer dried out in the summer of 1983.

The soil organic layer (A_0) in this study area shows a moder humus form with a poorly developed mineral soil horizon (A) which is about $1-2$ cm in thickness. This moder humus form belongs to the Leptomoder (Green, Trowbridge & Klinka, 1993). The A_0 layer develops on the A horizon and consists of L, F, and H layers ranging from $2-5$ cm depth. The soil organic layer (A_0) is a principal habitat for the soil animal populations. Soil fauna was dominated by micro-arthropods such as Collembola and Acari.

Litter bag experiments and sampling methods

The litter bag method was used to study the decomposition of *Chamaecyparis obtusa* needle litter and collembola succession (Crossley & Hoglund 1962). Freshly abscissed needles of *Chamaecyparis obtusa* were collected in January 1982, by shaking the trees over traps of nylon netting in the study area. Collected needles of *Chamaecyparis obtusa* were air dried at room temperature conditions. Litter bags measuring 10×10 cm in area with a mesh size of 1.0 mm were constructed. Three grams of air dried needles were placed in each litter bag. This litter mass approximated the annual needle litter fall of 3.5 t ha^{-1} in this study area.

Litter bags were set out in the $10\ m \times 20$ m plot which was divided into 20 subplots each $2\ m \times 5$ m in area. Ten subplots were used for the setting of litter bags. In each subplot, a $1\ m \times 1$ m in area was delimited for the setting of 12 litter bags. After the removal of the newly fallen litter, the litter bags were fastened to the forest floor by metal pins to prevent movement and to ensure good contact between the litter bags and the organic soil layers. Sampling of litter bags was carried out at 3 month intervals during the first 2-year period from May 1982 to January 1984. During the period from 1984 to 1986, litter bags were collected only in February. On each collection, 10 litter bags were collected from the study plot. A total of 110 litter bags were collected during the study period. On each sampling occasion, soil animals in the litter bags were extracted at a constant temperature of 35 °C (in a cabinet) using a modified Tullgren funnel extractor over 5 days in the laboratory.

Abundance of Collembola were studied in the soil of this plot. Sampling for soil animals was carried out on four occasions, i.e., February 1983, 1984, 1985 and 1986. Soil samples consisted of soil cores each 25 cm^2 in area and 4 cm deep and this sampling depth generally included the soil organic layer (A_0) which contained the vast majority of collembolan populations. Twelve soil cores were collected on each sampling occasion. Soil arthropods were extracted at a constant temperature of 35 °C (in a cabinet) using a high-gradient canister extractor (Takeda 1979). The extraction period was 6 days. Animals were collected in a solution of saturated picric acid and were sorted into groups under a binocular microscope. Soil animals were identified under a binocular microscope with a magnification of $400\times$.

Statistical analysis

Community structure is expressed by the following parameters: total number of individuals, diversity, species richness, and evenness. Community diversity was expressed by the Shannon-Wiener function as follows:

$$H' = \sum_{i=1}^{s} p_i \log_2 p_i$$

where s is the number of species collected from the samples, p_i is the number of i th species. Species richness was expressed by the number of species collected in each sample. The dependence of the estimates of community parameters on sampling size was negligible in this analysis where 10 sample units were used (Takeda 1987). Evenness was estimated using Pielou's index (Pielou 1966);
$J = H'/\log_2 S$, this value is unity when component species show completely even distribution.

Chemical analysis

Samples of initial and decomposing needles were dried at 80 °C to a constant weight and were ground in a laboratory mill to pass a 0.5 mm screen. Total nitrogen and carbon contents of needles were analyzed by automatic gas chromatography (C – N Corder, Yanagimoto Co. Tokyo, Japan). Nitrogen and carbon contents of the litter after a given period of decomposition were calculated by the following formula:
Remaining mass (percentage of original mass) = $C/C_0 \times DM/DM_0 \times 100(\%)$,
where C_0 is the initial concentration of nitrogen or carbon in the litter, C = concentration of nitrogen or carbon after a given period, DM_0 = original mass of dry matter, and DM = mass of dry matter after a given period.

Results

Decomposition processes of Chamaecyparis obtusa needles

Decomposition processes of *Chamaecyparis obtusa* needles were followed in terms of the changes in needle weights, carbon, and nitrogen mass. Fig. 1 shows the changes in mass of needles, and the carbon to nitrogen (C/N) ratios of the needles enclosed in the litter bags. Carbon mass mineralized during the decomposition process, while the nitrogen dynamics progressed through the leaching, immobilization and mobilization phases (Berg & Staaf, 1981). The decomposition process of needle litter followed three phase, i.e., leaching (from 0 to 3 months), the immobilization (from 3 – 20 months), and the mobilization (from 20 – 60 months).
The results show that litter provides three resource states for the colonization of collembola. The weights of needles enclosed in the litter bags represent the amounts of habitat available for the colonization of collembolan species. While the nitrogen and carbon contents of needles represent the litter quality for the colonization of collembolan species.

Abundance of Collembolan species in the soil

Abundance of collembolan populations in soil were studied during the litter bag experiments. Collembolan species usually show seasonal variation depending upon their life cycles and upon environmental factors (Takeda 1987). Collembolan community structure was studied over a 4 year period from 1982 to 1985. Winter population abundances of Collembola ranged from 33146/m^2 to 75486/m^2 over a 4 year period. Species composition of the collembolan community was summarized into species rank curves (Fig. 2). Collembolan community may be divided into dominant (over 1% of total populations), rare species

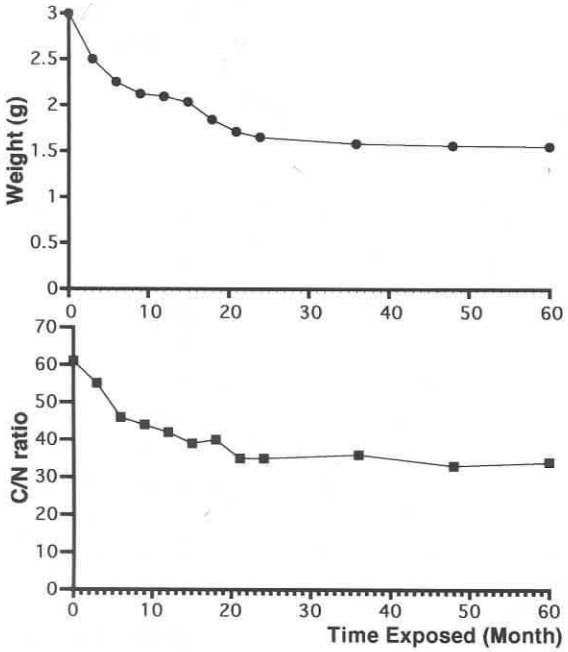

Fig. 1. (A). Changes in weight of *Chamaecyparis obtusa* needles enclosed in litter bags over a 5 year period. (B). Changes in C/N ratio over the study period. Decomposition process consisted of three phases; leaching, immobilization and mobilization

(1 – 0.1%) and very rare species (less than 0.1%) species groups. The collembolan community in the sol maintained by few dominant species, and the top 8 species accounting for 90% of total abundance. In spite of annual variations in the population abundances, there was no apparent shift in the abundance order between the abundance groups during the study period. Species composition was correlated between the 4 years and correlation coefficients ranged from r = 0.945 to 0.981. Thus, the identity of the dominant species, rare species, and very rare species were predictable over the study period.

Abundance of Collembolan species in the litter bags

Fig. 3 presents the relative abundance curve of the collembolan species collected from the litter bags over the 5 year period. In the litter bags, the collembolan community consisted of dominant species (over 10% of the total population), rare species (0.5 – 5%), and very rare species (less than 0.5%). The dominant species included *Tetracanthella sylvatica*, *Folsomia octoculata*, *Onychiurus flavescens*, and *Isotoma sensibilis* and accounted for 84% of total populations. With the exception of *I. sensibilis*, the dominant species in litter bags were also predominated in the soil habitat. In both soil and litter bags relatively few species dominated the collembolan community.

Colonization of collembolan species

A successional trend was observed in the species composition during the study period, and the patterns of colonization of species are shown in Fig. 4. According to the colonization patterns, the species may be classified into three groups. Group 1 consisted of the species *Folsomia octoculata*, *Onychiurus flavescens* and *Tetracanthella sylvatica*, which represented the predominant species throughout the decomposition stages of 5 year period. Abundances of these species were negatively correlated with the decomposition time.

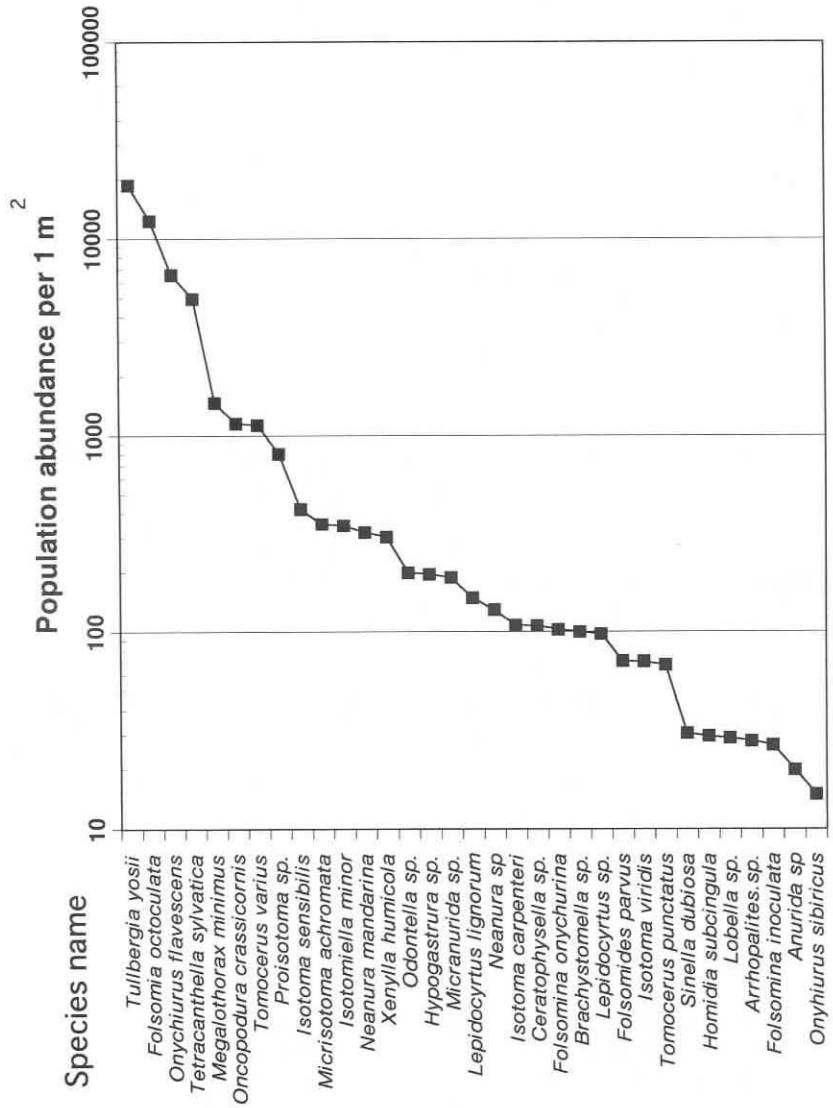

Fig. 2. Relative abundances of collembolan species in the soil habitat shown as mean abundance per 1 m^2 over a 4 year period

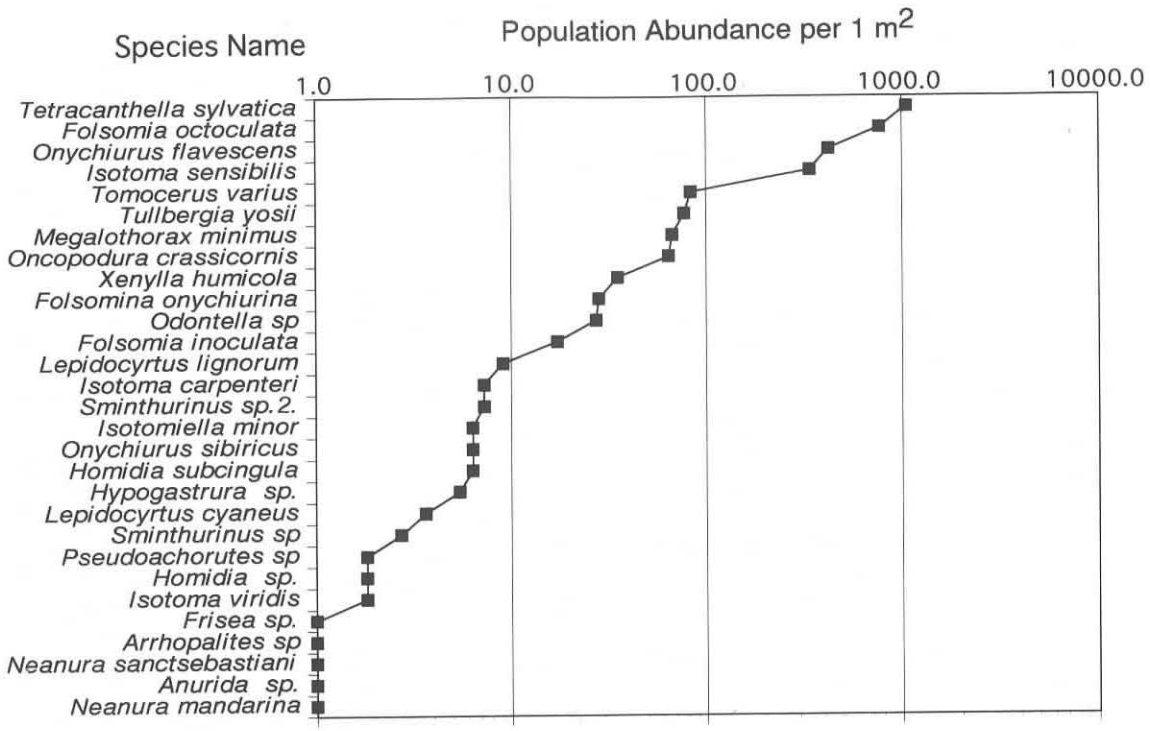

Fig. 3. Relative abundances of collembolan species colonizing the litter bags during the study period shown as a mean abundance per 1 m^2

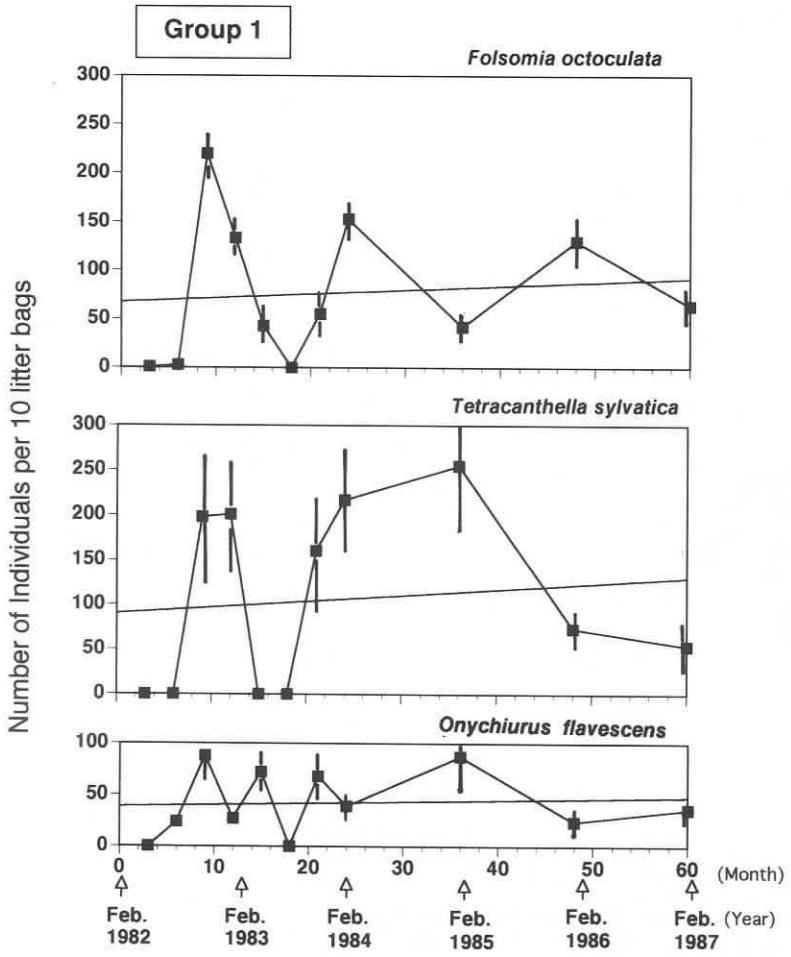

Fig. 4.1

Group 2 consisted of the early colonizing species and were abundant in the immobilization phase of decomposition. They mainly comprised of surface dwelling species, such as *Isotoma sensibilis*, *Tomocerus varius*, *Lepidocyrtus lignorum*, *Isotoma viridis*, *Sminthurinus sp.* and *Homidia subcingula*. The abundances of these species negatively correlated with the age of decomposing litter.

Group 3 consisted of the humus dwelling species *Tullbergia yosii*, *Isotoma carpenteri*, and *Folsomina onychiurina*. The later colonizing species showed increases abundances with the advance of decomposition.

The results showed a clear successional trend in the species composition during litter decomposition. The changes in the species composition might be related to the food-habitat preferences of the species associated with the decomposition stages of litter.

Changes in community structures

Changes in total abundance, diversity, evenness and species richness of the community in the litter bags are shown in Fig. 5. Twenty-nine species colonized the litter bags over the 5 year period and they accounted for 85% of the available species pool in the soil habitat.

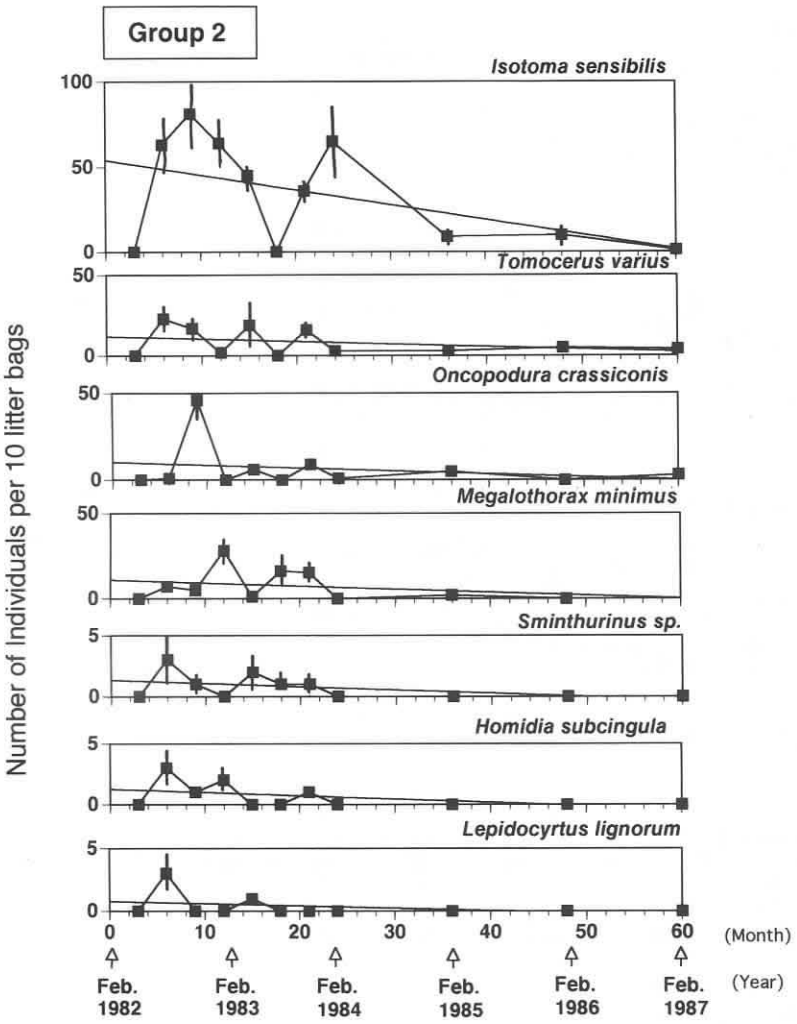

Fig. 4.2

The common soil species were all encountered in the litter bag community during the 5 year study period. The changes in abundance are characterized by a rapid colonization phase during the first 9 months from January 1982 to November 1983, then abundances declined during the following 9 months. The populations abundances were extremely low in the August samples when the litter layer was dry. After the summer population decline, the abundances recovered quickly in the October samples. Thereafter, the population abundances were rather stable over the rest of study period.
Diversity showed seasonal and annual variations during the decomposition processes of needles. Diversity was significantly correlated with species richness but not with the evenness component (Spearman rank correlation, $r = 0.69$, $P < 0.01$). The drought in summer resulted in the reduction of both abundances and species.

Turnover of species in the litter bags

Changes in species composition were examined in terms of emigration and immigration rates of colonizing species into and from the litter bags and were quantified by the turnover

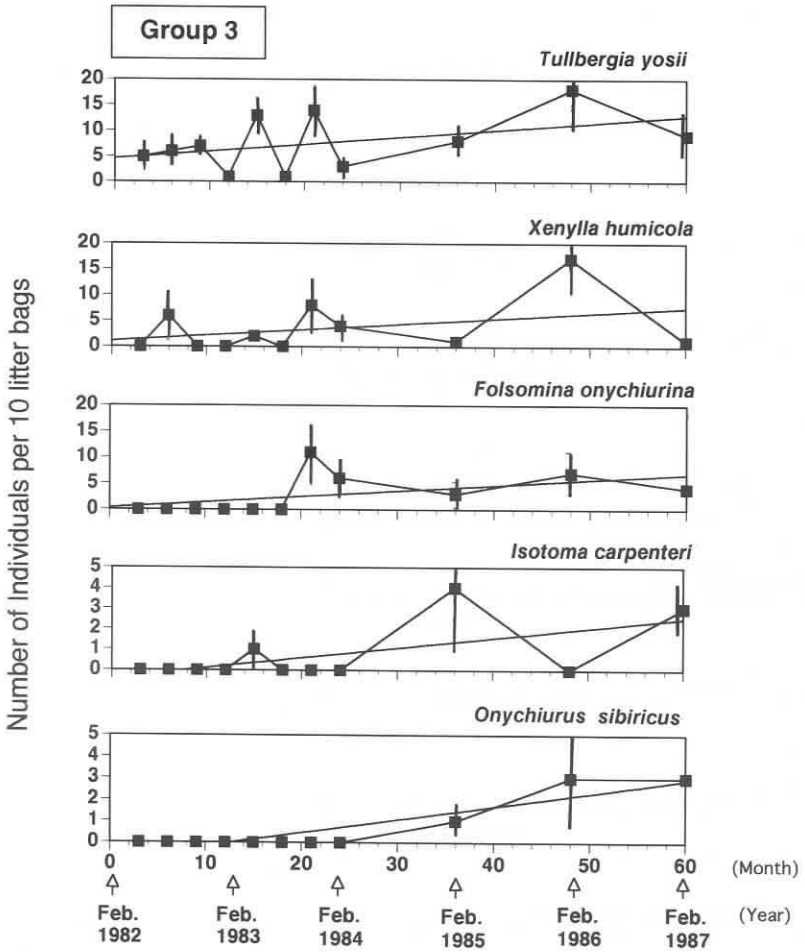

Fig. 4. Colonization patterns of collembolan species during the decomposition of litter over a 5 year period. Bars indicate the standard errors. Regression lines between dates and abundances indicate the successional trend of collembolan species. According to the successional trends, collembolan species were classified into 3 groups

rates of species. Species not present in the preceding sampling were considered immigrants and species absent were considered to have emigrated from the litter bags to the soil. The peaks of immigration of species occurred 3 moths after the setting of litter, at the completion of litter fall, and after the summer drought (Fig. 6). Whereas emigration showed peaks before the peaks of immigration in the first two years during which litter bags were in the L layer (Fig. 6).

Fig. 7 shows the turnover rates of species during decomposition. The percent turnover rates were calculated by the following formula; $(A + B)/C \times 100(\%)$ where A is the number of immigrant species, B the number of emigrant species and C is the number of species present at the two successive sampling dates.

Annual turnover rates of species are shown in Fig. 7 and ranged from 21 to 26% over the study period. The annual turnover rates were rather stable over the study period.

During the first 3 month interval, the species present in the litter bags were all new immigrants and the turnover rate was 100%. Thereafter, the turnover rates steadily decreased over a year during the decomposition processes of litter. After the end of the

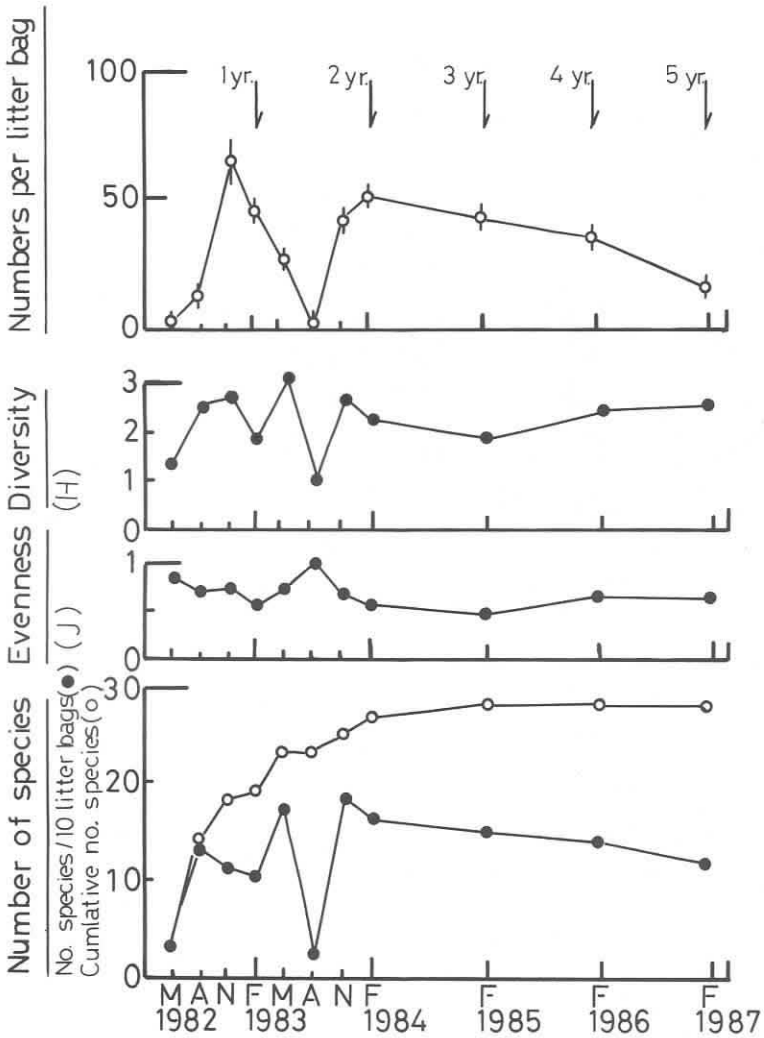

Fig. 5. Changes in community parameters; i.e. abundance, diversity index (H), evenness (J), and species richness (number of species collected at each sampling occasion) in the litter bags

litter fall period from November 1982 to February 1983, turnover rates increased. In August 1983, litter bag contained few individuals and species, because of the drought conditions in summer. The reduced populations recovered by the next sampling in October 1993. The disturbance effects of drought resulted in high turnover rates in summer 1993.

Discussion

The species composition of the collembolan community in the soil was consistent over the study period. Thus, this collembolan community might be maintained at an equlibrium state through the resource partitioning of collembolan species in the soil. In the pine forest near this study area, the collembolan community has been maintained at an equilbrium state over a 20 year period (Takeda 1987, Takeda 1995a). Bengtsson (1994) analysed the variability of temperate forest soil fauna communities between years and concluded that

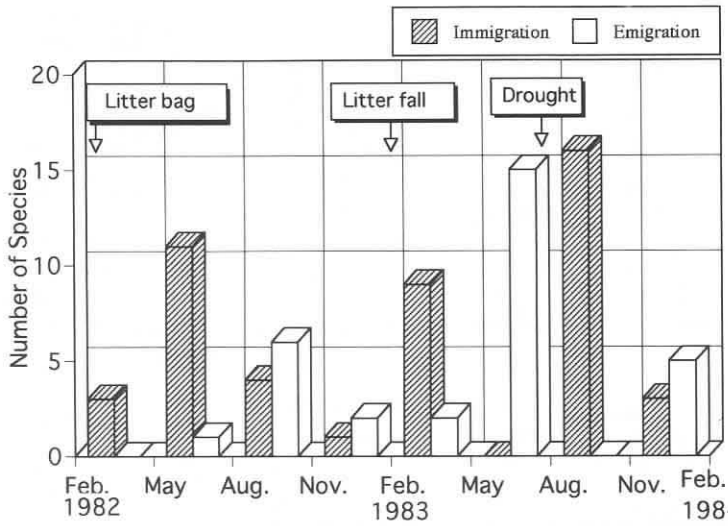

Fig. 6. Changes in immigration and emigration rates of collembolen species per 3 months' intervals. White and hatched column show the number of emigrants and immigrants respectively. Arrows indicate the litter bag setting, end of litter fall period, and drought during summer

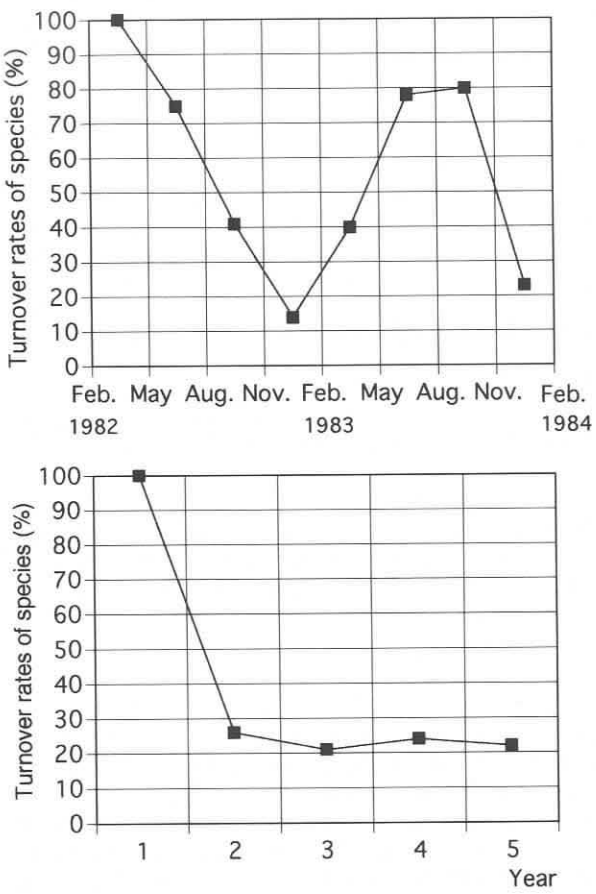

Fig. 7. Changes in turnover rates of species at 3 months intervals (A) and annual turnover rates (B)

soil fauna communities showed relatively small changes in community composition over the shorter time scale, i.e. less than 25 years. The predictive community may be related to the environmental stability in soils which is maintained by the processes, i.e., litter fall supply and decomposition processes (Takeda 1987; Ponge et al. 1993; Bengtsson 1994).

The community developed in the litter bags represents parts of the whole community in the soil. The litter bag communities showed seasonal and successional changes over the study period and these changes may be explained by reference to immigration and emigration of species into or from the litter bags during the immobilization phase of decomposition which lasted about 20 months. Ponge et al. (1993) showed the importance of litter supply in the maintenance of soil mesofauna communities by the experimental perturbations of litter supply in a temperate forest. The emigration and immigration patterns of collembolan species showed the importance of the litter fall, i.e., the renewal of habitat as the main driving factor in the succession of collembolan communities in the litter bags in the L layer (Takeda 1987).

Apart from the renewal processes of litter, the summer drought in 1983 affected the litter bag community, but this community quickly recovered after the drought. So, collembolan communities have a high resilience to perturbation factors, such as drought in the L layer. Collembola may escape the drought by vertical migration into deeper layers (Takeda 1978; Faber & Joosse 1993). After two years, litter bags move to the F layer where immigration and emigration of collembolan species showed no clear seasonal pattern related to litter fall, but continuous turnover of species still resulted from the decomposition of litter.

In this study the successional patterns of Collembolan were studied together with the changes in resource quality of litter, i.e. C/N ratio. During the decomposition processes, litter quality was changed as a result of carbon and nitrogen dynamics by the interaction between heterotrophic microbial and animal populations (Berg & Söderström 1979; Hasegawa and Takeda 1995) and modified the litter quality for the colonization of collembola.

In the leaching phase, collembolan abundances were low and composed few species. During the immobilization phase from 3 to 20 months, collembolan abundances increased and the collembolan community composed of dominant species group and surface dwelling species, such as *Tomocerus varius*, *Isotoma sensibilis*, *Homidia subcingula*, *Lepidocyrtus lignorum*, and *Sminthurinus* sp. Hasegawa & Takeda (1995) showed that *Lepidocyrtus lignorum* was a fungivore and might be abundant in the immobilization phase of decomposition. Hågvar & Kjøndall (1992) also showed that *Lepidocyrtus lignorum* was fungivorous and it was abundant in the early decomposition stages of birch litter. The surface-dwelling species of Collembola are grazers of fungal mycelium growing on and in the epidermal systems of needles and the grazing of these species may promote the activity of fungi by removing senescent fungal mycelium, and thus indirectly influence immobilization processes by fungal populations (Hågvar & Kjøndar 1981; Hasegawa & Takeda 1995). The fungivorous species may modifiy the decomposing litter by their feeding activities and facilitate the colonization of species in the mobilization phase.

The population of these species may be limited by environmental factors such as drought in the surface layer and by the short period of immobilization phase. The surface-dwelling species decreased with the advance of decomposition processes, and during the immobilization phase in the L layer, the litter fall was important for their maintenance.

During the mobilization phase in the F layer, abundances of the humus dwelling species *Tullbergia yosii*, *Folsomina onychiurina*, and *Isotoma carpenteri* increased with the advance of decomposition. These species were detritivorous or coprophagous (Takeda & Ichimura 1983; Ponge 1991) and were abundant in the moder humus. The later colonizing species may be contributing to the mineralization processes through their detritus feeding on the decomposed organic matter and faeces accumulated on the needle litter.

While *Folsomia octoculata*, *Tetracanthella sylvatica* and *Onychiurus flavescens* predominated through the decomposition processes of litter and in the soil habitat. *O. flavescens* specialized in detritivorous feeding throughout the decomposition stages of pine litter and its abundance

was increased in the mobilization phase (Hasegawa & Takeda 1995). Hasegawa & Takeda (1995) showed that *F. octoculata* was a dominant humus dweller in the pine forest and had an ability to switching diet from fungivorous to detritivoros depending on food availability during the decomposition stages.

Tetracanthella sylvatica are detritivorous and shows vertical migration from the surface layer in juvenile to the humus layer in the pre-adult and adult stages (Taked, 1978). This species may exploit the wide range of food and habitat resources because of the detritivorous feeding and the vertical migration ability and maintained dominance in the litter and soil communities.

The generalist feeders may utilize both the fungal populations in the immobilization, and the decomposed organic matter in the mineralization phases, and thus may contributed to the immobilization and mobilization processes of litter decomposition (Hasegawa & Takeda, 1995). Further the generalist feeders may maintain high population abundances in the litter and soil communities, because of the ability to switching diet depending upon the food availability. The detritivorous species may maintained their high abundances by their recycling use of decomposing materials in the moder humus form.

The successional pattern of the collembolan species is the response of individual species to the food and habitat conditions provided through the decomposition of litter (Takeda 1987; 1995; Vegter 1983). The litter bag studies clearly showed that the collembolan community was dynamically maintained by the responses of individual populations to the renewal of litter and decomposition processes of litter in the soil habitat. Litter decomposition helps maintain species diversity by providing a range of resource conditions during the immobilization and mobilization stages of decomposition.

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